Acta Œcologica
Œcol. Plant., 1987, Vol. 8 (22), n° 2, p. 113-126.

Seasonal changes of soil and plant water relations in Douglas-fir forest

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ABSTRACT

Measurements of sapwood relative water content (R_s) and soil water potential (ψ_s) were performed throughout the growing season 1985 in a 26-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) plantation located in the Apennines of Tuscany (Central Italy). Variations of sapwood water storage on a whole tree basis were estimated from R_s measurements. The evapotranspiration was periodically calculated from soil and sapwood water balance. During some days throughout the same period, twig water potential (ψ_t) and stomatal conductance (K_s) were measured on five trees of different d. b. h. at two crown levels.

From day 108 to day 276 R_s decreased from 87.4 to 38.5% which corresponds to a water depletion of 9.3 mm. In the same period ψ_s decreased from -0.007 to -0.992 MPa between 30 and 60 cm of depth. Between days 134 and 276 the contribution of sapwood water storage to the evapotranspiration was 1.9%. The maximum contribution from sapwood water storage to the evapotranspiration (11.2%) was found between days 228 and 242. An increase of R_s of 15.4% was observed between days 164 and 178.

Predawn twig water potential (ψ_p) varied from -0.675 MPa on day 163 to -1.064 MPa on day 276 with a maximum value of -0.409 MPa recorded on day 199. Over most of the sampling period ψ_s was notably greater than ψ_p. Only on day 276 ψ_p approched ψ_s.

ψ_t was always lower in the upper crown level. Generally, ψ_t decreased during the morning, reaching a minimum value around noon, and increased during the afternoon. No threshold level of ψ_t for stomatal closure occurred, not even when ψ_t was as low as -1.7 MPa.

KEY WORDS: *Douglas-fir - Water relations - Sapwood water storage - Evapotranspiration - Water potential - Stomatal conductance.*

RÉSUMÉ

Pendant la saison 1985 des mesures de la teneur relative en eau de l'aubier (R_s) et du potential hydrique du sol (ψ_s) ont été effectuées dans un peuplement de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) âgé de 26 ans situé dans les Appennins de la Toscane (Italie centrale). Les variations du contenu hydrique de l'aubier, pour l'arbre dans son ensemble, ont été estimées à partir des mesures de R_s. L'évapotranspiration a été calculée à partir du bilan hydrique du sol et de l'aubier. Pendant quelques jours de la même période, le potentiel hydrique des rameaux (ψ_t) et la conductance stomatique (K_s) ont été mesurés dans cinq arbres de différents diamètres à 1,3 m, à deux niveaux de leur cime.

Du jour numéro 108 au jour 276, R_s a diminué de 87,4 à 38,5% ce qui correspond à une perte d'eau de 9,3 mm. Dans la même période ψ_s a diminué de $-0,007$ à $-0,992$ MPa entre 30 et 60 cm de profondeur. Entre les jours 134 et 276 la contribution du contenu hydrique de l'aubier à l'évapotranspiration a été de 1,9 %. La contribution maximale du contenu hydrique de l'aubier à l'évapotranspiration (11,2 %) a été observée entre les jours 228 et 242. Une augmentation de R_s de 15,4 % a été observée entre les jours 164 et 168.

Le potentiel hydrique des rameaux avant l'aube (ψ_p) a varié de $-0{,}675$ MPa le jour 163 à $-1{,}064$ MPa le jour 276, avec une valeur maximale de $-0{,}409$ MPa enregistrée le jour 199. Pendant la majeure partie de la période d'échantillonnage, ψ_s a été considérablement plus grand que ψ_p. Seulement le jour 276, ψ_p s'est rapproché de ψ_s.

ψ_t a été toujours plus petit au niveau supérieur de la cime. Le potentiel ψ_t est descendu jusqu'à $-1{,}7$ MPa sans qu'on observe de fermeture stomatique.

MOTS CLÉS : Pseudotsuga menziesii - *Relations hydriques - Contenu hydrique de l'aubier - Évapotranspiration - Potentiel hydrique - Conductance stomatique.*

1. INTRODUCTION

A good knowledge of ecophysiological adjustments to changing environmental conditions is required to model water use and growth efficiency in forest plantations. Such a model can be an important tool to increase forest productivity by allowing an efficient manipulation of the site water balance (JARVIS, 1985).

Most studies on water relations of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands have been carried out in northern ecosystems (see LASSOIE, 1981). For that reason, a further contribution to this subject can be represented by researches performed in stands growing in different environmental conditions, *e. g.* in a mediterranean climate.

Careful experimental work on the effects of drought on water relations and on growth of Douglas-fir plantations growing in France, near to Nancy, was recently reported (AUSSENAC, 1978; AUSSENAC *et al.*, 1982; AUSSENAC *et al.*, 1984). The objective of the present work is to investigate the seasonal changes of tree water storage, twig water potential, leaf stomatal conductance and transpiration in response to the seasonal development of soil water deficit in a Douglas-fir plantation growing on the Apennines in Central Italy.

2. MATERIALS AND METHODS

2.1. STUDY AREA

The study was carried out in a 26-year-old Douglas-fir plantation located in Tuscany (900 m a. s. l., 43°46'43"N, 11°44'13"E). The earth is an acidic brown soil, 80-110 cm in depth, which can be classified as a *Distrochrepts* in accordance with the USDA's Soil Taxonomy (1975). The mean annual temperature is 9.4°C and the mean annual rainfall 1,248 mm. Temperatures and rainfall during the period studied and mean values of temperature and rainfall for the period 1951-1980 are given in table I. At the beginning of the measurement period the characteristics of the stand were as follows: number of trees per hectare: 2,044; mean height: 14.2 m; basal area: 41.7 $m^2\ ha^{-1}$; sapwood basal area: 23.2 $m^2\ ha^{-1}$; projected leaf area index: 9.3. Further description of the site is given by BORGHETTI *et al.* (1983).

2.2. MEASUREMENTS

– *Sapwood relative water content* (R_s): throughout the growing season 1985, sapwood cores were periodically extracted from four trees of different d. b. h.: 10, 15, 20 and 25 cm. The cores (4 mm of diameter) were extracted before 10:00 hours using an increment borer from the outer 2-3 cm of the sapwood at a height of 1.3 m above ground. For each tree, four positions at right angle on stem circumference were sampled. After extraction the cores were put in plastic vials and brought to the lab. Here the fresh weight of the cores was determined to the nearest 0.001 g. The fresh volume of the cores was determined on the basis of the Archimede's law, *i. e.* by the difference between weights in air and in distilled water. The samples were then dried at 60°C to constant weight and reweighted.

TABLE I. – *Temperatures (T) and precipitation (P) at the study area during the sampling period in 1985 and mean values of T and P (period 1951-1980) for the same months.*

Month	Daynumber	1985 T (°C)	1985 P (mm)	1951-1980 T (°C)	1951-1980 P (mm)
January	1- 31	−1.4	110	1.9	109
February	32- 59	3.5	50	2.6	113
March	60- 90	2.8	150	4.5	104
April	91-120	7.8	35	7.5	110
May	121-151	12.0	95	11.5	105
June	152-181	15.5	55	15.0	82
July	182-212	20.0	35	17.8	56
August	213-243	19.0	100	17.9	70
September	244-273	17.0	5	14.9	96

R_s (g cm^{-3}) was computed as follows:

$$R_s = \frac{W_f - W_d}{V_f - V_s} . 100 \qquad (1)$$

where W_f and W_d are the fresh and dry weights of sapwood, g; V_f is the fresh volume of the sapwood, cm^3; V_s (cm^3) is the volume of the solids, cellulose and lignin, computed from dry weight considering a constant density of 1.53 g cm^{-3} for solid materials (WARING & RUNNING, 1978).

– *The volume of water available for exchange* was calculated, for the stand as a whole, following the method described by WARING and RUNNING (1978).

The biomass of needles, living branches, stemwood and roots, the specific gravity and the sapwood fraction (the sapwood was easily distinguishable) of branches, stemwood and roots were obtained by the destructive analysis of twelve trees sampled in four diameter classes (BORGHETTI *et al.*, unpublished data) (table II).

In accordance with WARING and RUNNING (1978), we assumed that up to 80% of the water in the saturated sapwood is available.

The storage capacity of the needles were evaluated from the relationship between the needle relative water content (R_n) and the twig water potential. Arbitrarily, we considered as easily available water the fraction of water (24%) removed by a water potential of −2.0 MPa (fig. 1). R_n was measured on several samples of needles belonging to the twigs on which water potential was measured (see below). Immediately after collection the needles were stored in small air-tight plastic bags. Within few hours, the fresh weight was determined to the nearest 0.001 g. The needles were then brought to full turgor by placing them in distilled water at 2°C in the dark. After 24 hours the needles were carefully blotted with filter paper, weighed, oven-dried at 60°C to constant weight, and reweighed (WARING *et al.*, 1979). R_n was calculated as follows (WEATHERLEY, 1950):

$$R_n = \frac{W_f - W_d}{W_t - W_d} \cdot 100 \tag{2}$$

where W_f, W_t and W_d are respectively the fresh, turgid and dry weights of the needles, g.

– *The soil water potential* (ψ_s) was determined periodically throughout the growing season, by tensiometers in the range 0 to -0.08 MPa and with Wescor PCT-55 thermocouple psychrometers, using the Wescor HR-35 microvoltmeter, for values less than -0.2 MPa. Wescor psychrometers were calibrated using salt solutions of known osmotic potential in the range -0.2 to -2.8 MPa. ψ_s was measured at three places at different distances from the trees. At each place tensiometers and psychrometers were placed at a depth of 10, 20, 30, 50, 70, 80 and 110 cm, approximately. By a linear interpolation with respect to soil depth of all the tensiometer and (or) psychrometer measurements, ψ_s was estimated at 0.1 m soil intervals. For each soil horizon (0-30, 31-60 and 61-110 cm) retention curves (4,3 and 2 replicates for the three horizons, respectively) were obtained in the lab by pressure plate and sand box on undisturbed soil samples. Soil bulk density was equally determined (BUSONI & SANESI, 1986, personal communication). An average value of ψ_s and the water storage (W_s) was then calculated for each horizon (table III).

For each period an approximated water balance was computed as follows:

$$E_a = P \pm \Delta W_s \pm \Delta W_{\text{sap}} \tag{3}$$

where E_a is the actual evapotranspiration, mm; ΔW_s and ΔW_{sap} are respectively the changes in soil and sapwood water storage, mm; P is the precipitation, mm. Drainage, lateral fluxes and surface runoff can be considered small (SANESI, 1986, personal communication).

– *Leaf stomatal conductance* (K_s) and *twig water potential* (ψ_t) were measured at about 2-3-hour intervals from sunrise to sunset on some days in the period June-October 1985. Five trees of different d. b. h. (11, 14, 19, 25 and 28 cm) were sampled. For each tree, measurements were performed at two levels (13.5 and 11.5 m above ground) in the crown on three replicates, *i. e.* on three twigs belonging to the same branch at each level. At the upper level the twigs were fully exposed to sunlight, while at the lower level the twigs were shaded.

K_s was measured on current needles by a Li-Cor 1600 steady-state diffusion porometer. At the end of each measurement day the shoots were excised. The projected needle area was determined by a Li-Cor 3000 leaf area meter.

ψ_t was measured using a portable pressure chamber (SCHOLANDER *et al.*, 1965) on 1-year old twigs. After excision the twigs were kept in a dark and humid chamber. Measurements were made within 5 minutes from collection of samples. The pressure was increased at the rate of approximately 0.05 MPa s^{-1}. The end point was detected using a 12 × magnifying glass on the cut end of the twigs.

In three occasions (days 178, 199 and 247) and only for the 11 cm tree, ψ_t was measured on twigs taken from each whorl of the crown, to evaluate the vertical gradient of water potential.

– *Hourly values of actual evapotranspiration* (E_h) were calculated by the PENMAN (1953) combination equation (MONTEITH, 1965). Global solar radiation and vapour pressure deficit were measured respectively with a Moll-Gorczynski-type pyranometer and a ventilated psychrometer, placed horizontally at a height of 1 m above the canopy; soil heat flux was measured by two heat flux discs positioned horizontally below about 2 cm of litter. Net radiation was assumed to be 83% of global solar radiation (BORGHETTI & VENDRAMIN, 1983).

The boundary layer conductance was assumed to be 0.2 ms^{-1} irrespective of the wind speed (GASH & STEWART, 1975). The canopy conductance (K_c) was assumed as made up by the whole set of K_s connected in series and was estimated as follows:

$$K_c = K_{s1} \cdot L_1 + K_{s2} \cdot L_2 \tag{4}$$

where K_{s1} and K_{s2} are the average values of K_s and L_1 and L_2 are the cumulative projected leaf area index, respectively for the canopy portion exposed to sunlight and for the shaded one. The values of cumulative leaf area index were taken from BORGHETTI *et al.* (1986). When the vapor pressure deficit was less than 100 Pa the canopy was assumed to be wet and the evaporation was computed neglecting canopy resistance ($K_s \rightarrow \infty$).

When no measurements of K_s were available a potential rate of evapotranspiration (E_p) was computed by assuming a constant value of canopy conductance of 0.025 m s^{-1}, on the basis of the maximum measured value of K_s.

For the 11 cm tree, the sapwood relative conductivity (K, m^2) was calculated as follows (WARING & RUNNING, 1978):

$$K = \frac{q \eta l}{A_s \Delta\psi_t} \tag{5}$$

where η is the viscosity of xylem sap (N s m^{-2}); q is the flow rate (m^3 s^{-1}), obtained by multiplying E_h by the ratio between the sapwood basal area of the 11 cm tree and the stand total sapwood basal area; l is the path length (m); A_s is the sapwood cross sectional area of the 11 cm tree in m^2; $\Delta\psi_t$ is the vertical variation of ψ_t over the path lenght (N m^{-2}).

3. RESULTS AND DISCUSSION

The needle relative water content (R_n) exceeded in most cases 80% over a range of twig water potential (ψ_t) from 0 to -2.0 MPa (fig. 1). This agrees with the results obtained by WARING *et al.* (1979) in a 40-year-old Scots pine (*Pinus sylvestris* L.) plantation.

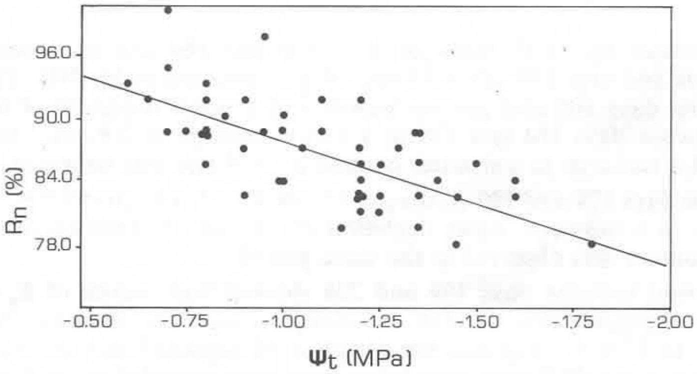

FIG. 1. — Relationship between needle relative water content (R_n) and twig water potential (ψ_t). ψ_t can be assumed in equilibrium with needle water potential (KELLIHER *et al.*, 1984). $R_n = 99.56 - 11.76\ \psi_t$, $r^2 = 0.69$.

In accordance with the results of WARING and RUNNING (1978) in old-growth Douglas-fir, the contribution of different organs to the tree available water storage follows this order: stem > roots > branches > foliage (table II). WARING *et al.* (1979) found that branches contribute to water storage more than roots in Scots pine.

Between days 108 and 276, R_s decreased from 87.4 ± 1.1% to 38.5 ± 2.1% (mean ± standard error) (fig. 2). From our estimates of sapwood water storage on a whole tree basis, this corresponds to a water extraction from sapwood tissues of 9.3 mm.

TABLE II. — *Biomass and water storage in the studied Douglas-fir stand* (BORGHETTI et al. *unpublished data*)

	Components				
	Foliage	Living branches	Stemwood	Roots	Totals
Dry weight (Mg ha^{-1})	14.6	23.3	142.9	45.3	226.1
Density (g cm^{-3})	1.00	0.56	0.47	0.56	
Total volume (m^3 ha^{-1})	29.8 (*a*)	41.6	307.1	80.9	429.6 (*b*)
Sapwood fraction	–	0.56	0.66	0.50 (*c*)	
Sapwood volume (m^3 ha^{-1})	–	23.3	202.7	40.5	266.5
Available water fraction	0.24	0.51	0.59	0.51	
Available water volume					
m^3 ha^{-1}	7.2	11.9	119.6	20.6	159.3
%	4.5	7.5	75.1	12.9	100.0

(*a*) Water volume in the foliage at saturation. Turgid weight of needles was 304 ± 6% of dry weight.

(*b*) Sum of total volumes of living branches, stemwood and roots.

(*c*) Conservative estimate.

Note : the stem sapwood density is 0.41 g cm^{-3}.

R_s decreased by 31.4% between days 108 and 164 and increased by 15.4% between days 164 and 178, after 53 mm of precipitation (table III). The decrease in R_s between days 108 and 164 corresponds to a water depletion of 6.0 mm, the increase between days 164 and 178 to a water recharge of 2.9 mm. Between days 164 and 178 a recharge in soil water content of 20.4 mm was observed.

Between days 178 and 199 R_s dropped from 71.4 ± 1.4% to 57.7 ± 2.9%, which corresponds to a sapwood water depletion of 2.6 mm. A decrease of 62.2 mm in soil water content was observed in the same period.

The period between days 199 and 228 showed high values of E_p but, at the same time, a considerable rainfall (63 mm), so that the decrease of R_s (from 57.7 ± 2.9% to 52.9 ± 3.5%) and the depletion of sapwood and soil water content (respectively 0.9 and 48.8 mm) were lower than these recorded in the former period.

From day 228 to day 242 a decrease of R_s from 52.9 ± 3.5% to 38.3 ± 2.1% (corresponding to a water depletion of 2.8 mm) occurred. In the same period a recharge of soil water content (19.9 mm) occurred.

Between days 242 and 276 rainfall was 5 mm and a soil water depletion of 44.6 mm was observed, while R_s remained low and practically constant ($R_s \simeq 38\%$). This is consistent with results, in Scots pine, of ROBERTS (1976) who found only a 1% of decrease in R_s on a tree which had an initial R_s of 38-41%. These small changes of R_s may reflect a substantial depletion of sapwood water storage.

From day 134 to day 276 the variation of sapwood water storage was 7.5 mm and accounted for only 1.9% of total E_a (table III). The maximum contribution of sapwood water storage to E_a was evaluated between days 228 and 242 (11.2%).

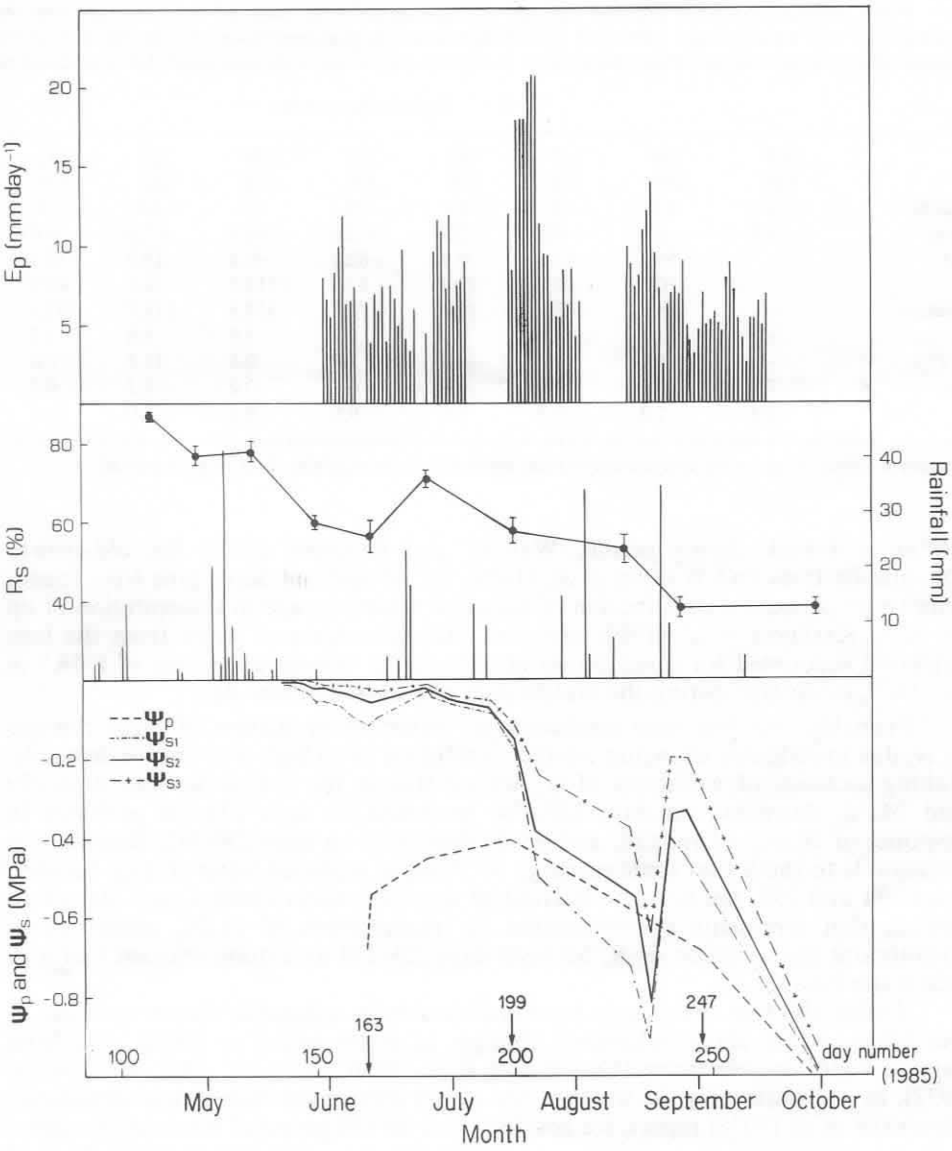

FIG. 2. — Seasonal variation of potential evapotranspiration (E_p), sapwood relative water content (R_s), rainfall, predawn twig water potential (ψ_p) and soil water potential ($\psi_{s1} = -.-.$, $\psi_{s2} =$ ———, $\psi_{s3} = -+-+$, respectively, for the three horizons from soil surface). During several periods E_p was not computed because micrometeorological measurements were lacking. Vertical bars indicate standard errors.

NNYAMAH and BLACK (1977) found, in a 20-year-old Douglas-fir forest, that the withdrawal of water from trunk storage accounted for 2% of evapotranspiration

TABLE III. — *Water balance terms for different periods.* ΔW_{sap} = *variation of sapwood water storage over each period;* ΔW_s = *variation of soil water storage over each period;* E_a = *actual evapotranspiration;* E_p = *potential evapotranspiration;* R_s = *sapwood relative water content. Water fluxes from the soil or vegetation to the atmosphere are considered negative.*

	Periods, daynumber								
From day	108	134	149	164	178	199	228	242	134
To day	134	149	164	178	199	228	242	276	276
a. Rainfall (mm)	96	11	4	53	23	63	42	5	201
b. ΔW_{sap} (mm)	−1.8	−3.4	−0.8	2.9	−2.6	−0.9	−2.8	0.04	−7.5
c. ΔW_s (mm)	–	−56.1	−17.2	20.4	−62.2	−48.8	19.9	−44.6	−188.6
d. E_a (mm)	–	70.5	22.0	29.7	87.8	112.7	24.9	49.6	397.1
e. E_p (mm) (*a*)	–	108.6	109.0	81.1	178.5	332.5	118.7	192.5	1120.9
f. E_a/day	–	4.7	1.5	2.1	4.2	3.9	1.8	1.5	2.8
g. $\Delta W_{sap}/E_a$ (%)	–	4.8	3.6	−9.8	3.0	0.8	11.2	0.0	1.9
h. ΔW_{sap}/day	−0.1	−0.2	0.0	0.2	−0.1	0.0	−0.2	0.0	0.1
i. ΔR_s/day	−0.4	−1.2	−0.3	1.1	−0.6	−0.2	−1.0	0.0	−0.3

(*a*) Cumulative values of potential evapotranspiration estimated from available data in each period.

during a 4-week drying period. WARING and RUNNING (1978) for old-growth Douglas-fir trees and WARING *et al.* (1979) for 40-year-old Scots pine trees found, over short periods, a contribution of sapwood water storage to transpiration of up to 50%. KELLIHER *et al.* (1984) observed that the release of water from the bole sapwood accounted for a maximum of 23% of the transpiration rate of a 16.7 m tall Douglas-fir tree during the middle part of a clear summer day.

Probably, our low time resolution prevented an evaluation of rapid changes of R_s due to suddenly changing weather conditions or to high evaporative demands. Taking accounts of variations of ψ_s, we see that in the period between days 229 and 242 ψ_s decreased on days 228-234, increased on days 234-238 probably in response of 24 mm of rainfall, and newly decreased on days 238-242. Because it is reasonable to think that some recharge occurred in sapwood water storage between days 234 and 238, the negative balance of sapwood water content over the whole period, that represents a contribution to transpiration of 11.2%, allows us to hypothesize the variation of R_s between days 228-234 as a quite relevant factor in tree water balance.

Within the tree, water can be withdrawn from extensible tissues external to the xylem, which show volumetric changes as water enters or leaves, and from sapwood inextensible tissue (CHALK and BIGG, 1956; STEWART, 1967; KOZLOWSKI, 1972). In our work, only the water stored within inextensible tissues was considered. HINCKLEY *et al.* (1978) report, for conifers, that 50-180 potential hours of transpiration can come from stem inextensible tissues, whereas only one potential hour of transpiration can come from stem extensible cells. WARING *et al.* (1979) report, for Scots pine, that sapwood tissues contain about 96% of total available water. Therefore, for conifers, it seems that sapwood water storage is more relevant to tree water balance than other storage locations.

From sapwood reserves water can be withdrawn by cavitation (*i. e.* by breakages in the water columns contained within tracheids, which become gas-filled) or by capillarity (ZIMMERMAN, 1983). As emphasized by PEÑA and GRACE (1986), the "capillary water" concept is plausible only where a high proportion of fibre-cells in xylem tissues provides the necessary cracks and crevices. This does not occur in Douglas-fir wood which largely consists of tracheids.

If cavitation were the main mechanism involved in the observed R_s variations, the increase of R_s between days 164 and 178 would be an interesting evidence for a refill of previously cavitated tracheids. It is not clear how this process can occur. In fact, tracheids which have become gas-filled cannot refill at the prevailing negative water potential because a zero or positive pressure is required to redissolve gas bubbles (Edwards, 1980; Peña & Grace, 1986). Some active mechanism can be postulated. Quoting from Edwards (1980), "parenchymatous tissue may permit the transfer of water to embolised tracheids. This could occur if diurnal variation in water potential was accompained by a phase lag in the osmotic adjustment of the parenchyma. After transpiration ceased at dusk, the osmotic potential of the parenchyma would induce additional entry of water into the cell. Subsequently as the osmotic adjustment was made, this additional water would be expelled, producing a small transitory positive pressure". It is worth remembering that in conifers each tracheid is in contact with one or more ray parenchyma cells (Esau, 1953).

R_s did not show significant variations between different positions within the trees in accordance with previous findings (Chalk & Bigg, 1956; Waring & Running, 1978). On the contrary variations between the trees were in some cases significant: R_s was often lower in the 10 cm tree. This may be related to a lower water uptake in suppressed trees.

Table IV. — *Seasonal variation of* (i) *predawn twig water potential* (ψ_p) *and daily minimum twig water potential* (ψ_m) *measured at two crown levels* (H=*higher*, 13.5 *m*; L=*lower*, 11.5 *m*); (ii) *average soil water potential* (ψ_s) *at different depths* (1=0-30 *cm*; 2=31-60 *cm*; 3=61-110 *cm*); SE=*standard error.*

		ψ_p (MPa)		ψ_m (MPa)		ψ_s (MPa)		
Daynumber		H	L	H	L	1	2	3
163		0.632	0.717	1.307	0.995	0.104	0.056	0.024
	SE	0.004	0.057	0.127	0.031	0.013	0.007	0.004
164		0.573	0.503	1.178	0.660	0.090	0.050	0.024
	SE	0.025	0.019	0.106	0.048	0.010	0.006	0.003
178		0.480	0.423	0.900	0.702	0.035	0.027	0.019
	SE	0.043	0.048	0.071	0.025	0.002	0.001	0.001
199		0.410	0.407	1.470	0.953	0.167	0.142	0.115
	SE	0.035	0.031	0.150	0.054	0.004	0.004	0.004
247		0.683	–	1.673	–	0.445	0.320	0.210
	SE	0.017		0.119		0.028	0.023	0.017
276		1.064	–	1.887	–	1.077	0.992	0.927
	SE	0.048		0.055		0.014	0.008	0.012

Predawn twig water potential (ψ_p) increased between days 165 and 199 when it was always lower than ψ_s. In the following period ψ_p decreased and dropped to its minimum of -1.1 MPa on day 276 in correspondence with similar values of ψ_s (figure 2 and table IV). As Kelliher *et al.* (1984) emphasized, the discrepancy between ψ_p and ψ_s could result from (i) the tree not being fully recharged, (ii) water uptake without transpiration and (iii) a transpiration dependent total soil-tree liquid resistance. It may be worth noting that no equilibrium was found between ψ_p and ψ_s during periods characterized by a progressive depletion of sapwood available water which means that no complete daily recharge probably occurred. On the contrary ψ_p approached ψ_s when sapwood water depletion stopped. KELLIHER *et al.* (1984) found, in Douglas-fir, that ψ_p was close to ψ_s when ψ_s was lower than -0.4 MPa.

Minimum daily twig water potential (ψ_m) varied considerably for variations of ψ_s above -0.2 MPa. For values of ψ_s lower than -0.4 MPa, little variations of ψ_m was observed. BALLARD and DOSSKEY (1984) found, for Douglas-fir seedlings, that needle water potential was little affected by soil drying.

The vertical gradient of ψ_t was -0.06, -0.08 and -0.19 MPa m^{-1} respectively on days 178, 199 and 247. For a 14 m tall Douglas-fir tree, under flux conditions, TAN *et al.* (1978) measured a water potential gradient of -0.12 MPa m^{-1}. The large gradient recorded on day 247 results from a considerable decrease of ψ_t in the upper crown part (fig. 3). This may be in relation with a reduced release of water from sapwood to the twigs which were more exposed to the evaporative demand. In fact, at this time, sapwood water storage was greatly reduced.

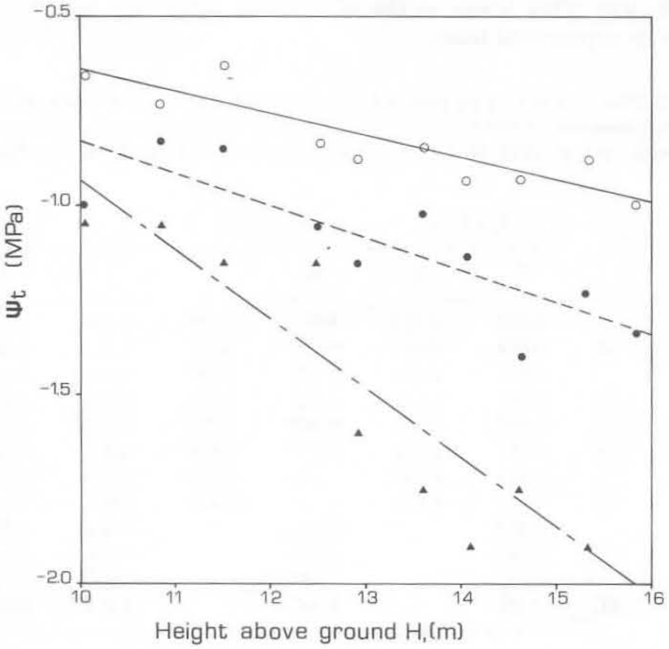

FIG. 3. — Vertical variation of twig water potential (ψ_t) on days 178 (○, $\psi_t = -0.13\text{-}0.06$ H, $r^2 = 0.81$), 199 (●, $\psi_t = -0.12\text{-}0.08$ H, $r^2 = 0.65$) and 247 (▲, $\psi_t = 0.79\text{-}0.19$ H, $r^2 = 0.82$).

Sapwood relative conductivity (K) was greater on days 178 and 199 with respect to day 247 (respectively 45.1, 52.4 and 19.5×10^{-12} m^2). The considerable decrease of K on day 247, when low values of R_s were measured (fig. 2), may be put in relation with a high proportion of cavitated tracheids which lose their transport function as become gas-filled. PURITCH (1971) in *Abies grandis* (Doug.) Lindl. and WARING and RUNNING (1978) in Douglas-fir found that K decreased as R_s decreased.

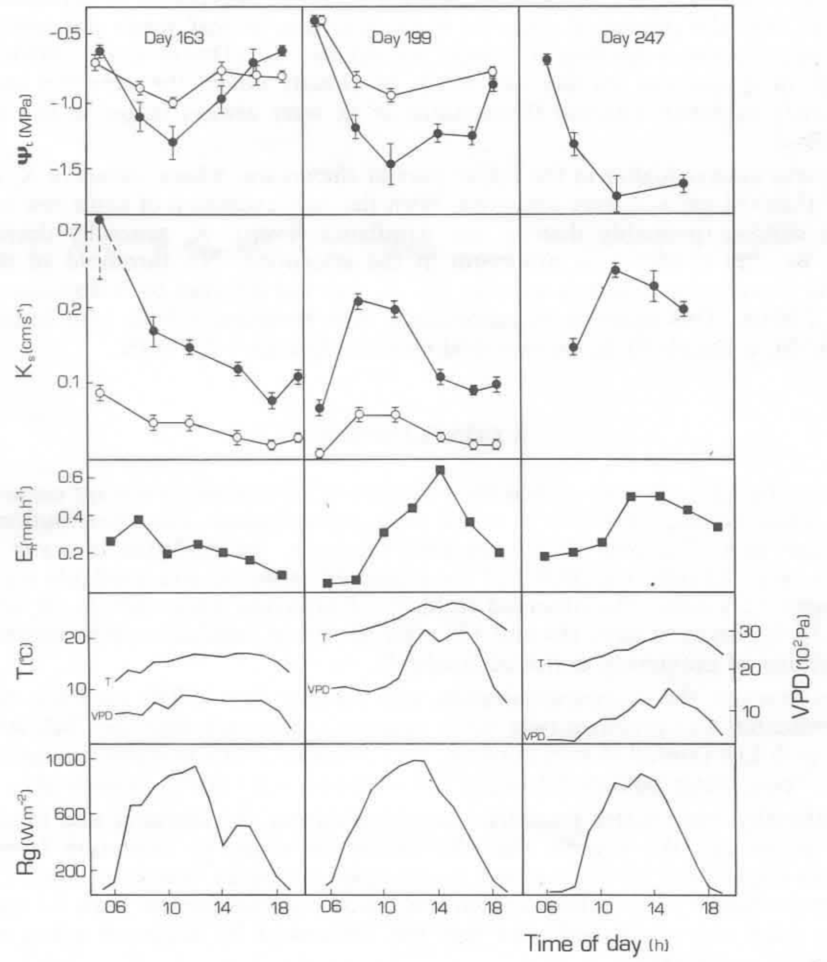

FIG. 4. – Diurnal variation of twig water potential (ψ_t), stomatal conductance (K_s; ● higher crown level; ○ lower crown level), evapotranspiration (E_h; ■), air temperature (T), vapor pressure deficit (VPD) and solar global radiation (R_g) on days 163, 199 and 247. Vertical bars indicate standard errors. E_h was 3.0, 4.2 and 2.1 mm day^{-1} respectively on days 163, 199 and 247.

The computed values of K were about three times higher than those reported by WARING and RUNNING (1978) for Douglas-fir trees, perhaps because we overestimated the water flow rate, calculated from values of E_h, for the 11 cm tree. At least in part, higher values of K may be due to the lower sapwood specific gravity recorded on our trees (0.41 g cm^{-3}) with respect to the value (0.45 g cm^{-3}) reported by WARING and RUNNING (1978).

Frequently ψ_t decreased during the morning reaching its minimum value around noon, at both crown levels (fig. 4). In the afternoon, ψ_t normally increased. This confirms previous results (Borghetti *et al.*, 1984). It can be supposed that a release of water by cavitation from sapwood sources might have relieved water stress in leaves. A link between ultrasonic acoustic emissions, interpreted as cavitations in tracheids, and the release of stress in leaves (increase of leaf water potential) has been observed on a sapling of *Thuja occidentalis* L. (Dixon *et al.*, 1984). No recovery of ψ_t occured on day 247 when, as already noted, the sapwood storage was mostly depleted. Diurnal fluctuations of ψ_t were always larger in the upper crown level.

K_s was always higher in the upper part of the crown, where values of K_s often greater than 0.1 cm s^{-1} were observed. With the only exception of some low values around sunrise (probably due to low irradiance levels), K_s generally decreased during the day reaching its minimum in the afternoon. No threshold of ψ_t for stomatal closure was reached. On day 247 K_s was not affected by a decrease of ψ_t to -1.7 MPa. This result is in accordance with Running (1976) who found, in Douglas-fir, a threshold ψ_t for stomatal closure close to -2.0 MPa.

4. CONCLUSIONS

Over the whole period studied the variation of the tree water storage corresponded to a low contribution (1.9%) to the evapotranspiration. This contribution was higher (up to 11.2%) over shorter periods. Globally, the depletion of water from sapwood was 9.3 mm, *i. e.* 58.4% of the estimated sapwood tree available water at saturation (15.9 mm). The observed recharge of sapwood water storage (R_s increased by 15.4% between days 164 and 178 after 53 mm of rainfall) may be interpreted as a refilling of previously cavitated tracheids.

On average, the evapotranspiration was 2.8 mm day^{-1}. The variation of soil water potential and predawn twig water potential was small until day 247. After a period with low rainfall (5 mm between days 247 and 276) soil water potential and predawn twig water potential dropped to -1.0 and -1.1 MPa, respectively.

Generally, twig water potential decreased during the morning and increased in the afternoon. We suggest that the release of water by cavitation from the sapwood might have releaved severe water stress in leaves. Stomatal conductance was always higher in the upper crown level, where values greater than 0.1 cm s^{-1} were in most cases recorded, and was not influenced by drops of xylem water potential to -1.7 MPa.

ACKNOWLEDGEMENTS

Research work supported by C.N.R. (Special grant I.P.R.A. — Sub-Project 1 — Paper No. 1032). We thank Dr. J. Grace (University of Edinburgh), Dr. A. Lindroth (Swedish University of Agricultural Sciences, Uppsala), Prof. P. J. Kowalik (Technical University of Gdansk, Poland) and two anonymous referees for critical reading of the manuscript. We thank Dr. E. Busoni and Prof. G. Sanesi (Centro di Studio per la Genesi, Classificazione e Cartografia del Suolo, C.N.R.-Firenze) for the measurement of soil physical parameters. The technical assistance of F. Bandini and A. Pierguidi is also gratefully acknowledged.

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